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Biogeosciences Discussions

Interactive comment on "Linking plant ecophysiology to the dynamics of diverse communities" *by* K. Bohn et al.

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First, we would like to thank the reviewer for the constructive and detailed comments. Some points raised by the reviewer were the consequence of unclear writing on our side, and we have tried to address this by rewriting many parts of the manuscript. We believe that by considering the comments of Reviewer #1, we were able to make this a much better and more nicely written manuscript.

General comments:

G1: The first and largest problem is that the writing is, in places, very difficult to follow. In particular, the description of the model requires much attention. (See specific comments for examples of where it is ambiguous). There is also some curious use of

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language in places, but this is easily corrected.

>The model description has been significantly rephrased, and a figure has been added to explain more clearly how DIVE works. We have been working with a native English language speaker to improve the language.

G2: The second main issue is that the authors somewhat overstretch the novelty of their modeling approach. Reading the discussion section, one might conclude that this is the first time anyone has ever attempted to include competitive interactions in a DVGM. Evidently, this is not the case, and the manuscript suffers from ignoring many recent interesting and relevant developments in the field of dynamic vegetation modeling (listed in the specific comments).

> We agree with the reviewer, DIVE is not the only model that attempts to include competitive interactions. We did not seek to claim that. In the view of the authors, the way in which DIVE represents competitive interactions is a new approach. Because it does not model interactions in a complex, spatially-explicit way, as do gap-models, nor the simple abstract way of simple DGVMs. DIVE models establishment, mortality, invasion and exclusion as independent processes being influenced by eco-physiological characteristics and different parameters. So the values of the rather aggregated model parameters in DIVE can be related to underlying eco-physiological trade-offs. We see this as one key innovation of DIVE.

G3: It would make for a much more interesting and acceptable paper if a section contrasting the JeDi/DIVE approach to other more sophisticated models was included.

>We would like to thank the reviewer for the comment. We have recognized that this indeed is a problem of the paper. We have included an additional paragraph in the discussion section that compares DIVE with other more sophisticated models.

G4: There are also repeated references to the models inclusion of 'ecophysiology', which in fact is reduced to highly simplistic notions such as relative growth rate, thus

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doing a disservice to the many models that include much more detailed considerations of physiological processes, and to it's inclusion of 'spatial' interactions, of which there is no mention in the methods. This over-stretching does a disservice to the authors, as the work is very interesting and useful as it is.

>This is an important aspect about which we should have been clearer. Indeed, DIVE does not explicitly incorporate ecophysiological details, nor does it model competition in a spatially explicit manner. However, first it explicitly states which aggregated ecophysiological properties, like relative growth rate, are needed to simulate community dynamics. Second, these aggregated ecophysiological properties can be calculated from models with more detailed physiological processes like JeDI, which do not need to consider the population dynamics. While it clearly is possible to construct models that at the same time incorporate ecophysiological detail and community dynamic processes, our aim was precisely to separate these parts as much as possible while keeping a well defined interface between them. This results in what we believe are models that are much more tractable, while keeping much mechanistic realism.

Specific comments:

P1: The title references ecophysiology, yet there is little in the way of ecophysiology discussed? How about something along the lines of "The relative importance of disturbance, resource competition and seed competition on community structure"

> We really like the idea for the title. We have changed the title to: "The relative importance of resource competition, seed competition and perturbations on community structure"

P2 L5: In the model methods, I don't see any evidence of a spatially explicit modeling approach. E.g. P6 L5 "Establishment of new individuals is modelled by assuming that all seeds from all PPSs are well mixed over the grid." Can you clarify what you mean by this?

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> We do not use an individual based model; there is no notion of age in the model. In DIVE, each PPS is represented much simpler and can be seen as a green box. Also we do not work with a specific spatial resolution. To calculate establishment dependent on the seed flux, the physical assumption is that seeds are uniformly distributed. To avoid confusion with a spatial explicit approach we have changed the text "We link growth and reproduction characteristics from different plant strategies, that emerge from climatic constraints, to their competitive abilities and calculate explicitly their spatial dynamics." into "We link growth and reproduction characteristics from different plant strategies, that emerge from climatic constraints, to their competitive abilities and calculate their spatial dynamics implicitly.

P2 L14: "We conclude that linking ecophysiological characteristics of vegetation to competition is a valid approach to determine population dynamics" is a somewhat vague conclusion, arguably has been achieved before by gap models, and does not represent the novel parts of this study, which are, for me, the focus on how explicit parameterisation is required to control the strengths of seed and resource competition.

> Indeed, our approach is new in that we can independently control the strengths of seed and resource competition and perturbation. But also we presented a new model approach that abstracts spatial explicit processes such as light competition into an implicit approach that uses emergent rather than parameterised plant strategy characteristics to model establishment, mortality, invasion and competition. We have changed the text "We conclude that linking ecophysiological characteristics of vegetation to competition is a valid approach to determine population dynamics." into "We conclude that growth and reproduction characteristics emergent from ecophysiology can be used to model the influence of varying strength of seed competition, resource competition and perturbation as independent processes on community dynamics with an approach of intermediate complexity."

P3 L15: "Thus it seems necessary to understand how plant species composition changes along with competitive interactions, performance and climate to be able to

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predict how vegetation responds to environmental change." This sentence is rather awkward and I am not sure what it means. Perhaps you need to delete the 'along'?

> We changed the sentence: "Consequently, in order to be able to predict how vegetation will respond to environmental change, the competitive interactions between species that may alter as well need to be captured."

P3 L21: "One option . . . to include population dynamics in vegetation models such as the Dynamic Global Vegetation Model (DGVM) LPJ (Sitch et al., 2003) at the cost of increased model complexity." Arguably, some, albeit more abstract, representation of population dynamics is already present, by definition, in all dynamic vegetation models. I think you need to be explicit here about the precise change you are suggesting.

> Our approach is less complex than gap models (where the individual environmental conditions depend on the geometry of neighbouring individuals) but more process-based than simple population dynamics in DGVMs (where often e.g. tree-grass coexistence can only be obtained by definition). DIVE is intermediate since it links growth and reproduction characteristics in order to calculate the spatial dynamics of different plant strategies implicitly. We consider seed competition, resource competition and perturbation as independent processes affecting population dynamics. We have rewritten the last part of the introduction section in order to explain where DIVE is situated within existing approaches.

P3 L26: "Can you clarify here what is meant by 'successful'. My understanding is that JeDi selects plant types that are successful in the absence of competition, i.e. those whose physiological traits make it possible for them to successfully reproduce in a given climate. This information is needed to understand what further processes are simulated by DIVE.

> Yes, this understanding is correct. JeDi selects plant strategies that are successful in the absence of competition. The successful plant strategies must be able to cope the climatic condition so that they have some biomass and have reproduces their initial

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seed mass. We have removed this sentence here to concentrate in the introduction more on the population dynamics. But we do explain this in the methods section.

P4 L4: “due to its characteristics” needs to be more specific.

> Here we meant growth and reproduction characteristics. We have rewritten this section in the introduction.

P4 L9: “perturbations summarise” should probably be “perturbations include”. Also I don’t think either disease or herbivory, or arguably fire, should be categorized as abiotic processes as they all depend on biotic drivers.

> We agree with the reviewer and have changed the text: “Perturbations include disturbances such as fire, disease, herbivory or abiotic stress.”

P4 L10-15: It may be true that the PPS’s can be categorized, but is it necessary to categorize them, or to include that statement here?

> We intent to remind the reader that plant strategies differ in their ability to colonise or compete and do in the results and discussion use these terms. However, here it is not necessary and we removed it.

P4 L20: Can you give a citation for a rule-based model here? Also, not all models are rule-based, and DIVE is not the only model that can simulate population dynamics, as this sentence might be interpreted

> We did not seek to claim that DIVE is the only model that can simulate population dynamics. What is new is how the population dynamics are calculated. We have included a more comprehensive discussion in the Introduction, paragraph 4 to explain where DIVE is situated. Also we discuss the rule-based models in the discussion section, where we contrast DIVE to other models.

P5 L4: How is biomass per m2 a constant feature of a plant type? Surely this will vary with environmental conditions? Maybe it changes through time as the output of JeDi,

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and I have misunderstood, but this needs clarifying.

> Biomass per m2 of occupied area is an output variable of the JeDi Model, used in DIVE as input. With our simplified setup it is constant. However, the total biomass of the ith PPS is determined by Ai * BMi in DIVE, and Ai changes in time. We have cleared up the text, and use the additional Figure 2.

P5 L4: Should the rate of seed production be linked to the amount of vegetation of a given plant type that is present, rather than just time?

> Yes, it is actually linked. When the germination fraction is calculated, we use Ai * fseed,i (Eqn. 4) to get the actual seed flux (fseed,i is given per m2 of occupied area, as well as the other input variables of DIVE). We have not changed the text.

P5 L6: What is 'specific' about 'specific mortality rate'?

> We used specific because each PPS has a separate mortality rate. To avoid confusion we have removed this word.

P5 L8: Most DGVMs, and indeed all vegetation models, do not use this two-step approach, and combine the estimation of physiological validity in the same model as competitive interactions. How does the two step approach help here?

> This paper can be understood as a proof of concept for the DIVE model. The two step approach facilitates the analysis of the role of competition and perturbation, as we can run DIVE alone. We explained the idea in the methods, section model application.

P6 L6: What are the units of Abare, and indeed, of all the variables introduced in this model description? What is specific about the specific growth rate, and how/why does that relate to seed establishment?

> Table1 lists all variables with their units. Additionally we have inserted the units in brackets after the introduction of a variable in the text. Abare and Ai are fractional, and in that respect dimensionless [m2/m2(of total area)]. We have removed "specific",

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see response P5 L6. We have added Figure 2 to understand establishment, see also response P5 L4.

P6 L7: If the growth rate of each PFT is a simple parameter, I think it is stretching it somewhat to claim that the model links 'ecophysiology' to plant dynamics. By reducing the processes of light capture, carbon assimilation, autotrophic respiration and resource allocation into a single parameter, much of our understanding of plant ecophysiology is ignored. It is, of course, a perfectly reasonable simplification, for the purposes of understanding either diversity or competitive interactions, but I think the authors should be less bold in their claims as a result.

> Please see response G4.

P6 L9: Where did fseed come from? What are its units?

> The parameter fseed,i is produced by JeDi. Its units are gC/m2 of ccupied area/unit time (see Table 1), please see response P5 L4. It determines the amount of carbon that will be allocated to the production of seeds for each meter squared that the plant strategy occupies for each unit of time.

P6 L9: Is 'germination fraction' the number of seeds produced by a given PFT that germinate, or the fraction of total germinating seeds that come from each PFT? If this is actually 'seed limitation', can it not just be called that instead? I am having difficulty understanding this section. It is not clear, for example, how the existence of seeds from other PPS's affects the rate of colonization of bare ground. This section needs careful re-writing.

> The germination fraction gi describes how much of the total area could be covered, if the all seeds from a PPS would germinate. The physically assumption behind is that gi determines what proportion of settled seeds can germinate on bare area. Seeds from other PPS affect the rate of establishment only indirectly. If at time step a PPS has a high establishment then bare area becomes limited in the next time step. Seed com-

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petition is modeled, in that the seed flux of each PPS does matters for establishment. Under neutral seed competition the seed flux does not matter. We have rewritten the description of establishment in the methods.

P6 L21: Does the phrase 'as they grow toward their adult size' need to be in this sentence?

> We added Figure 2 to explain this and removed this statement as it leads to misunderstandings.

P6 L22: Change "biomass per occupied m is given with the input" to "biomass per occupied m2 is an output of the JeDi model and an input to DIVE"

> We have changed the text as suggested.

P6 L21-24. At the end of this sentence "Establishment includes the increase in fractional coverage of new individuals as they grow towards their adult size, but not the increase in biomass per occupied m2" .I am expecting to learn about how biomass increases. However, we then turn back to consideration of area "This rate of increase in area is captured with a PPS specific growth rate, κgrow,i" We then return to consideration of biomass: "The growth rate is determined by the biomass per occupied square meter BMi and the productivity of a seedling". This results in very high degrees of confusion. Also, if fnpp is the growth rate only of the seedling, why does the text then discuss how it controls the development of an adult tree? If Kgrow is constant with age, is it not just the 'tree' (or plant) growth rate?

> We have significantly reworded the text to better explain the relationship between area and biomass. Please see response: P5 L4 and P6 L21

P7 L14: Where do the respiration and litter fluxes come from? The JeDi model? I think you need to explain why you think mortality is the ratio of carbon loss to biomass here. Are the conclusions of McGill and Gillooly applicable to a problem of this scale? Do they match existing observations of tropical tree mortality?

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> Respiration and litter fluxes are output variables from JeDi, that serve as input parameters to DIVE. DIVE is made to be a general approach, consequently using broad assumption appropriate for global scales and many different plant species (trees as well as grasses). The analysis of McCoy and Gillooly is relevant in that the relationship between size and mortality, with larger organism having higher mortality rates, seems to be a general pattern (please see response to review #2 Eqn 7) that can be used in global models. However, if we were to use DIVE to analyse specific biomes such as the tropics, in the light of Wright et al. 2010 a better parameterisation could be needed. They concluded i.a. that mortality rates of tropical tree species are in general independent of the maximal height. We have changed the text in the methods and also discuss the work of Wright et al. 2010 in limitations and benefits.

P7 L15: "In order to investigate the effects of perturbations, we incorporate the reaction of perturbations in altered mortality by the factor cMort , that scales mortality:" This sentence makes no sense to me at all.

> We have rewritten this sentence: "We explore the effects of changing the intensity of perturbations via the use of a cmort parameter that alters the mortality rate. Higher values for cmort would correspond to more severe perturbations that would lead to an increase in mortality."

P7 L21: Note that mortality rates are calculated _in an analogous manner_ to growth rates

> Thanks, we have changed this.

P8 Eqn 8: I don't think you have defined 'k' at any point. Apologies if I missed it.

> We have changed the eqn. 8 to include "from k=1 to n", where n is the number of PPS. We have added n in Table 1.

P9 L5: What kind of process-based model? What processes would it include?

> We have changed the in Model application: "In principle DIVE could be integrated into

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a process-based vegetation model that serves the necessary input data for DIVE. Also empirical data could potentially be used. By using a process-based vegetation model that is based on ecophysiological principles, the produced model output that serves as DIVE input would make sense in that the PPS characteristics suit each other.

P9 L23: It is necessary to have both the table and the figure? I would argue in favour of dropping the table, and reducing the length of the discussion of the PPS characteristics.

> We think both are necessary because the figure helps to compare the different PPSs, while the numbers in the table are needed to reproduce our results. But we have reduced the number of digits.

P10 8-10: If "The PPS i occupies the fractional area A of a grid cell" and A(t=0)=1, for all PPS's the sum of the 'A's will be 5. I'm sure this is not the case, but it needs clarification. Also, if "in an initially bare area: Abare =1" are you suggesting that this simulation is one of these cases? How does that work if all the area is occupied by plants already? This needs re-writing aswell, I think.

> Ai(t=0)=0, leads to g_i (t=1)=0 for all PPSs, consequently nothing will grow. Therefore we need to start with Ai x fseed,i > 0 and so we use as initial seed flux Ai x fseed,i = fseed,i (Eq. 4). We have changed the text to explain this.

P10 L14: "we conduct multiple sensitivity analyses"

> We have changed the text: "We conduct a series of sensitivity analysis experiments."

P12 L22-28: Figure 5 is very interesting, and could be discussed at greater length.

> We have added a section in the discussion to discuss this deeper.

P13 L8: In the follow_ing

> We have changed that.

P14 L15: What do you mean by the 'global scale' and 'grid level' comparison here?

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> The text has been changed: “While in the global study of Fisher et al. 2010 altered mortality had no significant effects for plant functional type composition, we found perturbations controlling mortality to be an important factor of how and what steady states are reached. Since our study is conducted only on a tropical climate, we can expect that effect on the global scale, too.”

P15 L2: “. . . with DIVE we are able to distinguish resource from seed competition and can show that both processes have different effects, especially when perturbations come into play” This is, in my opinion, the most important point in the study, and should be included in the abstract.

> Yes, we agree with the reviewer. That is one of the most important points in the study, we rewrote the abstract to include it.

P15 L17: The DIVE approach is potentially (and not necessarily) superior to that contained in area-based DGVMs, but many DGVMs are not area based at the present time and already include the explicit role of competition for resources between plant types. How does this method compare in terms of computational capacity and ecological realism to more sophisticated models (SEIB, LPJ-GUESS, HYBRID, ED, aDGVM etc.) In my opinion, the main advance in this study is to investigate the relative roles of seed and resource competition. Most of the newer models do not pay much attention to see competition (with some exceptions) and the concept that the strength of competitive exclusion and seed competition are is a complex processes requiring parameterization is not well understood in this literature. To simply state that this approach is better than a rule-based approach is a disservice to the intellectual content of this study and to willfully ignore the development of newer vegetation modeling approaches in the last decade.

> We agree with the reviewer, and added a special section in the discussion comparing DIVE to other approaches.

P16 L2: The same point – not all DGVMs use rule-based approaches.

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> Section is rewritten. Please also see response P15 L17.

P16 L16: I would call mortality a 'process' rather than a 'response'

> We agree, mortality is a process. Here we talk about the effect of cMORT that is a multiplier of the mortality rate. Therefore we talk about cMORT as a parameter that changes the effect of mortality. To make this point clearer, we have changed the text "The perturbation parameter cMort in DIVE implicitly models a range of different perturbations as a constant response, while they could be modelled also stochastically." into "The perturbation parameter cMort in DIVE will affect the mortality of a PPS. While this process could be modelled stochastically (Values of cMORT could vary over time, as done often for disturbances), here we apply a constant perturbation parameter."

P16 L18: I don't think perturbation rates are uniformly unknown. I would say they are poorly quantified.

> We have changed the text: "However, perturbation rates are poorly quantified and the values might be different in specific regions of the Earth."

P16 L19: 'necessary' rather than 'needed'

> The text has been changed, please see sentence in response P16 L18.

P16 L26: There are no data in this paper, so I do not think we are in a position to comment on the likely strength of competitive exclusion. Whether the modelled succession is plausible is not a trivial comparison.

> We agree with the reviewer. Indeed it will very difficult to compare modelled succession with observed succession. Therefore we rephrased the sentence: "We showed that including competition leads to plausible population dynamics. However in different climates the strength of seed and resource competition might be different and it will be challenging to find them."

P17 L2: response to what?

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> We cleared this up: “Ecological communities might never get into a steady state (Wallington et al. 2005) and time until communities respond to such perturbations can be very different (Sandel et al. 2010).”

P17 L5: estimates of what?

> The text has been changed: “Especially when predicting biomass under climate change scenarios, estimates of biomass are uncertain (Rammig et al. 2010) and depend on vegetation composition (Fisher 2010).“

P17 L7: Most models of vegetation do not assume steady states. I don’t think the ability to capture transient states is the main strength of this approach.

> We agree with the reviewer. Recent approaches usually do not assume a steady state. We have changed the text: “While the JeDi model, that we used to produce the input for DIVE, assumes climate equilibrium, together with DIVE transient states of vegetation are captured.”

P17 L12: “The model could be run with a certain setup” is an unnecessary sentence. What kind of observations could help to constrain the values of the competition parameters? I would argue that they are extremely difficult to determine until we have a better understanding of the functional (rather than species) diversity of existing ecosystems. It would be good to have more discussion on this point.

> This a non trivial issue, since in different climatic regions seed competition strength, resource competition strength and levels of perturbation might be different. In a next paper we want to address this issue. Our idea is, that modelled biomass and species richness could be compared to data obtained from different biomes. Applied to future climate, care would need to be exercised in that the previous climate’s parameters may not necessarily be valid. For example, perturbations such as fire and water stress may increase under different climates. However simply tuning the model to produce such pattern is only one half, the remaining issue is then what are the mechanism behind

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that. - We discuss this point in limitations and benefits.

P17 L18: Again, there are very few models that assume a steady state. I don't think you need to include this point.

> Thanks for the comment, we removed the statement and changed the sentence: "The motivation was to capture implicitly spatial dynamics."

P17 L18: The model does not simulate spatial dynamics in the sense that I understand. Models of tree migration (e.g. TREEmig – Lischke et al.) simulate how seeds are distributed in the landscape with a spatial component. Further, individual based models (SEIB, LPJ Guess, SORTIE) retain spatial information on the location of individual plants. This model does neither, and so I consider that this reference is inaccurate.

> Again, we did not want to state that we model explicitly competitive dynamics. We do not use a spatial 3D resolution. We rather use a 1D implicit modelling approach. We rewrote that statement in the conclusion and hope that throughout the rewritten and added sections our idea becomes clearer.

P18 L8: Again, DIVE/JeDi are not the only models that can simulate population structure as affected by plant charecteristics.

> Yes, we agree, and again did not want to say that. We changed the text: "The motivation was to capture spatial dynamics implicitly by using emergent growth and reproduction properties of different plant strategies with an approach that would be scalable for producing predictions for vegetation response to both local and global changes. DIVE distinguishes between seed and resource competition. Both can be controlled independently as well as perturbations."

Interactive comment on Biogeosciences Discuss., 7, 8215, 2010.